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THE BIOLOGY AND TAXONOMY OF THE PORTULACA OLERACEA L. (PORTULACACEAE) COMPLEX IN NORTH AMERICA

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ABSTRACT

Portulaca oleracea L. is a polyploid, cosmopolitan weed with a broad physiological adaptability. It is morphologically variable, grows rapidly, is self-compatible producing large numbers of seeds that have a long survivability. The variability is expressed in a series of local populations that exhibit clinal variation geographically. Data obtained from the literature on the biology of the species are compared to previous taxonomic interpretations in order to develop a more functional taxonomic treatment of this polymorphic species.

Key Words: Portulaca oleracea, taxonomy, species biology, cytology, seed morphology

INTRODUCTION

Portulaca oleracea L., purslane, is one of the world's most aggressive weeds, having been noted as the eighth most frequent plant (Coquillant, 1951) and one of the ten most noxious weeds (Singh and Singh, 1967). It is common in cultivated fields, gardens and lawns, as well as waste areas, driveways, eroded slopes and bluffs, occurring from sea level to 2600 m (Vengris et al., 1972). It is most common in the temperate and subtropical regions, although it grows in the tropics and into the higher latitudes. Legrand (1962) reports it from 45° north latitude and 40° south latitude, while Zimmerman (1977) extends this to 51° on the American continent and 54° on the European continent. Recently this had been extended to 58° in the Canadian province of Alberta (J. G. Packer, pers. comm.). The origin of the species is uncertain and new data and interpretations have made the accepted theories questionable. De-Candolle (1886) considered it to be Old World (India) spreading into the New World. Ridley (1930) suggested that P. oleracea is a native of deserts or desert-borders of North Africa, and Hagerup (1932) cited the Sahara as its center of origin. Although not citing this species specifically, Geesink (1969) concluded that the ancestral lineage of the genus is in Australia. In North America this species has been considered as introduced from the Old World.

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It is included in Dioscorides' first century herbal (Gunther, 1959). Gray and Trumbull (1883a) summarized the evidence for a pre-Columbian existence of purslane in North America by noting that Columbus' diary (1492) had an entry reporting purslane in Cuba. Also Nuttall in Missouri and Long in what is now Colorado, reported purslane before settlers could have transported it from the east. Gray and Trumbull (1883b) allude to a possible Viking entry, possibly from Iceland into Greenland and finally into Newfoundland. There is no current report of this species occurring in either Iceland or Greenland. Additionally, Scott (pers. corresp. 1992) reports that purslane is not currently part of the flora of Newfoundland. These data support the latitudinal limits presented above. Byrne and McAndrews (1975) report on the finding of P. oleracea pollen and seeds in sediment samples of a lake in southwestern Ontario, Canada, dating from the period 1430-89 A.D., with more intensive analyses extending the range from 1350 to 1539 A.D. Their explanation of this occurrence is based on man's use of the plant. Indians living in the vicinity of the lake possibly collected plants from fields and washed them in the lake, depositing the pollen and seeds in the water. In addition to the purslane residual, maize pollen (Zea mays) and pollen and seeds of sunflowers (Helianthus annuus) were also found in the same layer of sediment. Furthermore purslane seeds have been recovered from archaeological sites in Kentucky which date back to the first millenium B.C. (Watson, 1969) and from southern Louisiana dating back 1500 years (Walker, 1936). These data indicate an indigenous development or movement of the species across the continents during prehistoric times (Chapman et al., 1974). Richard Yarnell (pers. comm. 1992) suggests that P. oleracea has been in North America perhaps since 7000 B.C. Further insight on the success of this species can be gained by examining the biology of P. oleracea reported on below from the work of several investigators.

MATERIALS AND METHODS

Herbarium specimens were obtained from: ARIZ, ASC, ASTC, ASU, BRY, CAS, COLO, DAV, DES, DUR, F, FLAS, FSU, FWM, GH, HPC, ISC, JEPS, KANU, KS, KSC, KSP, LAF, LL, LSU, MICH, MNA, MO, MU, NLU, NMC, NO, NY, OKL, OKLA, PAUH, RSA/POM, SD, SMU/BRIT, TAES,

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TAMU, TEX, UARK, UC, UCSB, UMC, UNCC, UNLV, UNM, US, USF, UT, UTC, UTEP, and UVST. Live specimens were collected from California, San Bernardino Co. (Valley between Granite and Van Winkle Mts. on Kelbaker Rd., 7 mi. N of I-40; Pass between Vontrigger Hills and Hackberry Mts., E side of Lanfair Rd., 11 mi. N of jct. Goffs Rd.); New Mexico, Bernalillo Co. (base of light pole, San Felipe St., Old Town, Albuquerque); Illinois, Jackson Co. (Lawn, Pyramids Complex, S. Rawlings St., Carbondale); North Carolina, Mecklenburg Co. (Garden, 5724 Doncaster Dr., Charlotte); and South Carolina, Beaufort Co. (Along sidewalk, Coligny Plaza, Hilton Head Island). Chromosome squashes were obtained by placing root tips in 0.1% colchicine for 1.5 hr, fixing in 3:1 alcohol-acetic acid overnight, hydrolyzing in 1 N HCl for 12 min. at 60°C, placing in Feulgen stain for four hours and squashing in dilute Aceto-carmine stain to provide cellular detail. Four plants from each site were studied. Photographs were taken using a Zeiss Axioskop equipped with Normarski differential interference contrast optics. Seed surfaces were examined and photographed, after sputter coating with gold-palladium on a Hummer V, with a Jeol JSM-35CF scanning electron microscope.

THE SPECIES BIOLOGY OF PURSLANE

The species is mostly an annual, but may be perennial in the tropics. The leaves are alternate, subalternate or opposite, obovate to spatulate with an obtuse or truncate-emarginate apex. The leaves may range from 40 mm by 15 mm up to 60 mm by 25 mm in fertile soils. Apical verticils have 2-5 leaves, with usually 4. Axillary hairs are missing, inconspicuous, or barely visible. Flowers are in a group at the end of the stem subtended by 4 leaves. The two sepals are fused to the base of the ovary and may grow into a wing-like carina of 3-4 mm long that can cover the ripening fruit. There are (4)5(6) yellow petals ranging from 3-10 mm long by 2-8 mm wide with 6-15 (3-20) stamens. The style branches are 3-6, the capsule ranges from 4-9 mm, dehiscing at or just below the middle. Seeds are black, 0.6-1 mm, usually with granulate (Figure 1) to flat stellate (S-undulate) (Figure 2) surfaces and small tubercles along the dorsal curvature. However the seed surface can also be raised stellate (S-undulate) with tubercles on the lateral seed surfaces (Figure 3) or exhibit intermediate patterns (Legrand, 1962; Geesink, 1969; Kim, 1989).

Zimmerman (1976) reported on the growth characteristics of weediness in P. oleracea, in comparison with P. pilosa and P. grandiflora. Common purslane branches almost immediately after germination and therefore spreads out in its growth pattern quicker than the other two species. It produced flowers in day lengths from 4-24 hours, with a direct correlation between increased illumination and flower production (except for 20 hr.). There was no flowering photoperiod. Capsule production and overall plant growth (dry matter) also increased with increasing day length. When tested with nonvarying light and varying temperatures, ranging from 16°/11°C (day/night) up to 28°/22° the number of capsules increased by a factor of 1.3. When tested for productivity in varying moisture regimes, purslane was able to mature capsules in soils of high or low moisture. Zimmerman (1977) reported on the breeding system and seed physiology. Purslane flowers did not open on cloudy days or days below 21°C. When opened, they remained open for 4 hours. The flowers were self-fertile, and under experimentation did not exhibit apomixis. No insects visited the flowers. Mulligan (1972) saw no insect visitors to purslane flowers over a three-year study. These same features of autogamy, no apomixy and lack of insect pollinators were supported by Kim and Carr (1990a). Miyanishi and Cavers (1980) reported evidence of at least 5% outcrossing in purslane and Mulligan (1972) and Zimmerman (1976) proposed that outcrossing is accomplished by wind. Our examination of the flowers showed the pollen to be sticky, not a characteristic of a wind borne process. Kim and Carr (1990b) reported a natural hybrid in which P. oleracea was one of the putative parents. In Zimmerman's study (1977), seed germination remained constant, at over 90%, over a 2.5 yr. period. Vengris et al. (1972) reported the following percentages of germination for seeds: 0.2 year-old, 39%; 1 year-old, 78%; 7 years-old, 59%; 14 years-old, 59%. Muenscher (1955) reported that purslane seeds were viable for at least 40 yr. Zimmerman (1977) found over 60% seed viability after passing them through a house sparrow (Passer domesticus). Light was required for germination, but the temperature requirements were variable. Purslane seeds can germinate at 10°C and in a test of overwintering, over 82% of the seed survived a winter in Michigan. Singh (1968) showed that seeds collected in India germinated over a range of 10°-40°C, but did not germinate at 50°C. Vengris et al. (1972) noted that a purslane plant

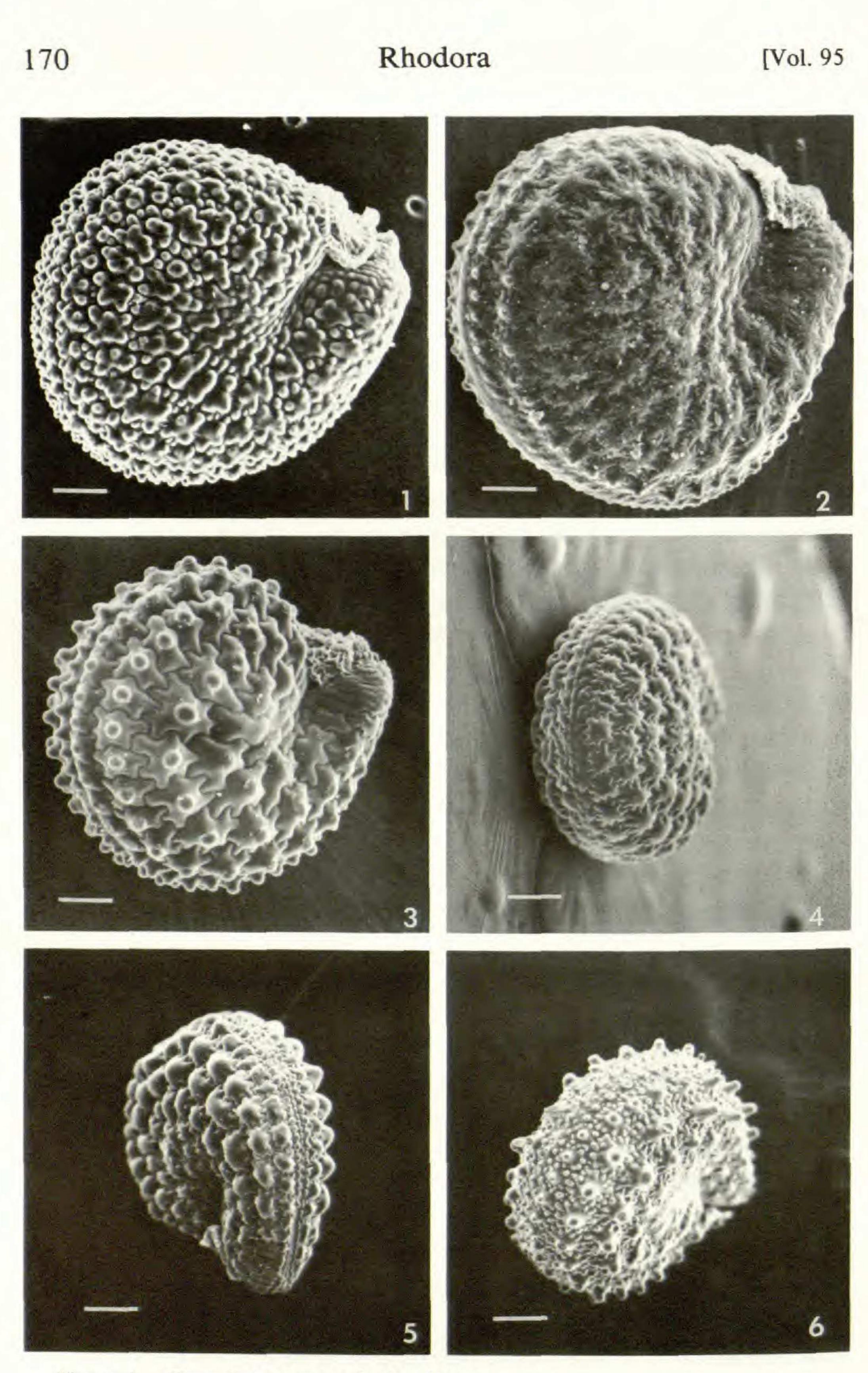


Figure 1. Granulate pattern in P. oleracea.

Figure 2. Stellate (S-undulate) pattern in P. oleracea.

Figure 3. Stellate (S-undulate) tuberculate pattern of a specimen labelled P. retusa that matches Engelmann's lectotype.

of 28 cm produced 6723 seeds after 5–6 weeks of growth (e.g., the first flush of flowers). Zimmerman (1976) estimated that over an entire season a purslane plant can produce 101,625 to 242,540 seeds.

From the above, *Portulaca oleracea* can be characterized as a weed of open, disturbed habitats with nearly a world-wide adaptability and distribution. It grows rapidly, producing flowers, fruits and a large number of seeds within six weeks of germination. It has a wide tolerance of photoperiod, light intensity, temperature, moisture and soil type. Seeds germinate under conditions that enhance the survival of seedlings. The self-compatible breeding system, longevity of seeds, resistance of the seeds to the digestive processes of animals, and the overwintering capacity of the seeds help ensure its survival and distribution. These characteristics have a bearing on the taxonomy of the species as described below.

TAXONOMY

In an ancient, cosmopolitan species in which autogamy is the rule, local populations possibly reflecting variable morphological and physiological traits can be expected. The fact that the species has not been split into a plethora of microspecies (as defined by Stace, 1989) is surprising. An examination of the two most recent comprehensive monographs, Legrand (1962) and Geesink (1969), show the following: Legrand's treatment of the American species has only three synonyms at the specific level under *P. oleracea*. Geesink's treatment of the Indo-Australian and Pacific species places only two in synonymy. There thus appears to have been a reticence to subdivide *P. oleracea*. Whether this is due to a lack of understanding of the genus or of an appreciation of the variability of this species is unknown. In reality, both reasons probably are contributors. An examination of the works of Legrand and Geesink, cited above, shows several examples of taxonomic/no-

Figure 4. Raised stellate (S-undulate) pattern without tubercles labelled as P. retusa.

Figure 5. Raised stellate (S-undulate) pattern with incipient tubercles, labelled as *P. retusa*.

Figure 6. Granulate pattern with tubercles labelled as P. retusa.

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menclatural problems in species less widely distributed than P. *oleracea*.

Gorske et al. (1979) provide some insight into the world-wide variability of P. oleracea in their numerical taxonomic study. Forty-four ecotypes representing both weedy and cultivated forms from 18 countries were analyzed, using 36 morphological characteristics. The cultivated forms, used for food, were obtained from commercial seed sources in Egypt, France, Norway and the United States. No physiological or cytological characters were included in the study. Three different methods were used in the analysis: the unweighted pair group method of clustering using arithmetic averages, principal component analysis and stepwise multiple discriminant analysis. All three analyses gave similar results and show that the cultivated forms can be separated from the weedy populations. The weedy populations can be divided into three distinct groups: cool temperate, warm temperate to subtropic and humid subtropic to tropic. The Canadian populations fit into the cool temperate. The populations from the upper U.S. fit into the warm temperate to subtropic group while those from the lower U.S. fit into the humid subtropic to tropic group. The effects of selection for cultivation (forming a separate group) are apparent, as well as are the lack of smaller groupings over large geographic areas. That this study over such a large geographic distribution with a large representation of ecotypes showed only three groups that fit a clinal variation from warm humid subtropic to cool temperate, and did not segregate into groups that could be considered as microspecies supports our conclusion that P. oleracea is best viewed as a single polymorphic species. As discussed below under the cytology, within the U.S., three cytotypes occur. There is no well-defined cytological correlation with the cool temperate, warm temperate to subtropic and humid subtropic to tropic groups. Portulaca oleracea is a weed that exhibits wide geographical, morphological, physiological and cytological plasticity, an obvious reason for its success.

Several names have been proposed as segregates within this complex. One such is *P. neglecta* Mackenzie and Bush, based on a specimen collected by Bush in Courtney, MO in 1900. Type: U.S.A. Missouri, Jackson Co., 24 Aug 1900, *B.F. Bush s.n.* (Holotype: MO!, Isotype: NY!). Courtney no longer exists, having been eliminated by the growth of Kansas City. An examination of the type specimens and seven other specimens identified as *P. neg*-

lecta (the only ones received from all loan requests) from MO, KS and MI have vegetative features and seed surfaces typical of P. oleracea. The leaves are large, 40 mm by 15 mm; but this is typical for large specimens of P. oleracea. In the original description of P. neglecta, Mackenzie and Bush (1902) differentiated the new species from P. oleracea on the basis of earlier opening flowers; larger size of the plant; larger, broader and thinner leaves and more numerous stamens. He said that P. neglecta occurred in MO, KS and AR and is probably what has been called P. retusa Engelm. in MN, MO and KS. In correspondence from Aug to Nov 1909, from NY, attached to a herbarium sheet without a plant, N. L. Britton asked Bush for fresh material for study. Bush's reply was that the species grew in rich, sandy bottoms and the floods of the past two years had apparently destroyed the populations. Bush also added that the other form, typical P. oleracea, grew in pastures and looked very different. From this exchange, we conclude that the large specimens were either escaped cultivated forms or represented local populations from wet habitats in which the plants grew larger than those in drier pastures. All of the features Mackenzie used to differentiate P. neglecta are easily modifiable vegetative features. No specimens have been reported since these initial collections. We conclude that P. neglecta Mackenzie and Bush is P. oleracea L. and that the former

name should be in synonomy under the latter.

In another study of this species, Danin et al. (1978) proposed nine subspecies of Portulaca oleracea, based on seed size, seed surface and chromosome number, with the cytotypes having distinct geographic separation. We recognize the need to express infraspecific variation (Matthews et al., 1991, 1992a); and as Stace (1989) concluded, "the provision of a name attracts attention to a taxon." In the genus Portulaca each species must be studied to determine which characters are consistent and persistent, a difficult process. Due to the almost cosmopolitan distribution of P. oleracea with its adaptability to many habitats, the propensity for self pollination, long term seed viability and the lack of specialized seed dispersal mechanism, this species exists in a myriad of local populations that exhibit morphological and/or physiological variability peculiar to each deme. Since the species is succulent, taxonomic characters have been sought in the more durable structures, such as seed surface. In some species of Portulaca these surfaces appear to be consistent and predictable but in the wide-

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spread *P. pilosa* the seed surface morphology was neither consistent nor predictable over the geographical range of the species (Matthews and Levins, 1985, 1986; Matthews et al., 1992a, 1992b). Legrand (1962) stated that seed surface characters, particularly in *P. oleracea*, are not dependable because the variation is unpredictable. Each population often presents a different pattern. He concluded that seed surface cannot be used to separate even varieties because infinite transitions are produced between non-tuberculate and tuberculate and between rugose and stellate sur-

face patterns.

We find this same situation in *P. oleracea* where there is a mosaic of seed surface morphotypes. We do not think that these morphotypes should be treated as subspecies. We tend to follow in principle the concept of subspecies as defined by Stuessy (1989) where a subspecies should have several conspicuous morphological differences, should be cohesive geographically and largely allopatric, with multigenic control of the differences. Additionally, there is the possibility of hybridization along contact zones but with markedly reduced fertility of hybrids.

In a subsequent study by Danin and Anderson (1986) on the subspecies of P. oleracea in Florida, five subspecies representing three cytotypes were identified and their distributions mapped. Most of these five overlapped both in geographic distribution and in chromosome number. In addition there were several specimens that could not be assigned to any subspecies, implying more variation than had been circumscribed in the nine subspecies already described. These were suggested to be potential hybrids. This does not mean that seed surface morphology is worthless as a taxonomic character. In some genera it has proven useful in defining subspecies. Walters (1964) in Flora Europaea recognized four subspecies of Montia fontana (Portulacaceae) based on seed surface morphology and very sharply distinct geographic distributions. Here the morphological character is enhanced by allopatric distributions, a situation not present in the study by Danin and Anderson (1986) of P. oleracea in Florida.

We conclude that *P. oleracea* exists as a polymorphic species and is not divisible into subspecies based on seed surface as the primary morphological trait.

Another part of the *P. oleracea* complex is *P. retusa* Engelm., described in 1850 (Gray, 1850) from specimens collected by Lindheimer in the granitic region of the Liano (sic), Llano of western

Table 1. Herbarium sheets of P. retusa Engelm. considered as lectotypes.

- 1. P. retusa Engelm., Aug 1849. Engelmann s.n. (MO, 122802), specimens numbered 8871 and 8872.
- 2. P. retusa Engelm., no date. Engelmann s.n. (MO, 122803).
- 3. P. retusa Engelm., no date. Engelmann s.n. (MO, 122804).
- 4. P. retusa Engelm., 1849. Engelmann s.n. (NY).
- 5. P. retusa Engelm., 1849. Engelmann s.n. (NY). Obtained from Princeton in 1945.
- 6. P. retusa Engelm., 1849. Engelmann s.n. (NY).
- 7. P. retusa Engelm., Aug 1849. Englemann s.n. (GH).

Texas. Engelmann grew plants from seeds sent to St. Louis and distributed specimens to GH and NY. He distinguished *P. retusa* from *P. oleracea* by the former having broader retuse leaves, broader calyx, distinctly tuberculate pale seeds, and larger style with 3–4 short stigmas. He noted that the number of stamens was variable, up to a maximum of 15-17 and that the flowers opened earlier in the day than those of *P. oleracea*.

With the difficulty in assessing herbarium specimens in this genus and with the morphological variability of P. oleracea as reported above, the floristic treatments for areas in which both species were reported have relied primarily on the tuberculate seed surface and 3-4 stigmas to distinguish P. retusa (Wooton and Standley, 1915; Wilson, 1932; Kearney and Peebles, 1942, 1951; Shreve and Wiggins, 1964; Harrington, 1964; Correll and Johnston, 1970; McDougall, 1973; Martin and Hutchins, 1980; Barkley, 1986; Henrickson, in prep.; Felger, in prep.). In an earlier study, Matthews and Levins (1986) published an SEM of the seed surface of P. retusa showing a tuberculate, S-undulate (raised stellate) pattern as typical for this species. This illustration is reproduced as Figure 3. In the preparation of this treatment for North America, we gathered 121 specimens labelled P. retusa. We wanted to compare these to the holotype, but found that Engelmann had failed to designate such and there have been no lectotypes designated. There are seven specimens which qualify for consideration as type material, Table 1.

Sheet one has two plants. One is from the Engelmann collection of Aug 1849 with Engelmann's personal label: "From Texas seeds, cultivated St. Louis." Seeds are present on the specimen, which is noted on the sheet as no. 8871. The other plant on the sheet, with the no. 8872, was collected by Wright in Oct 1849 in western

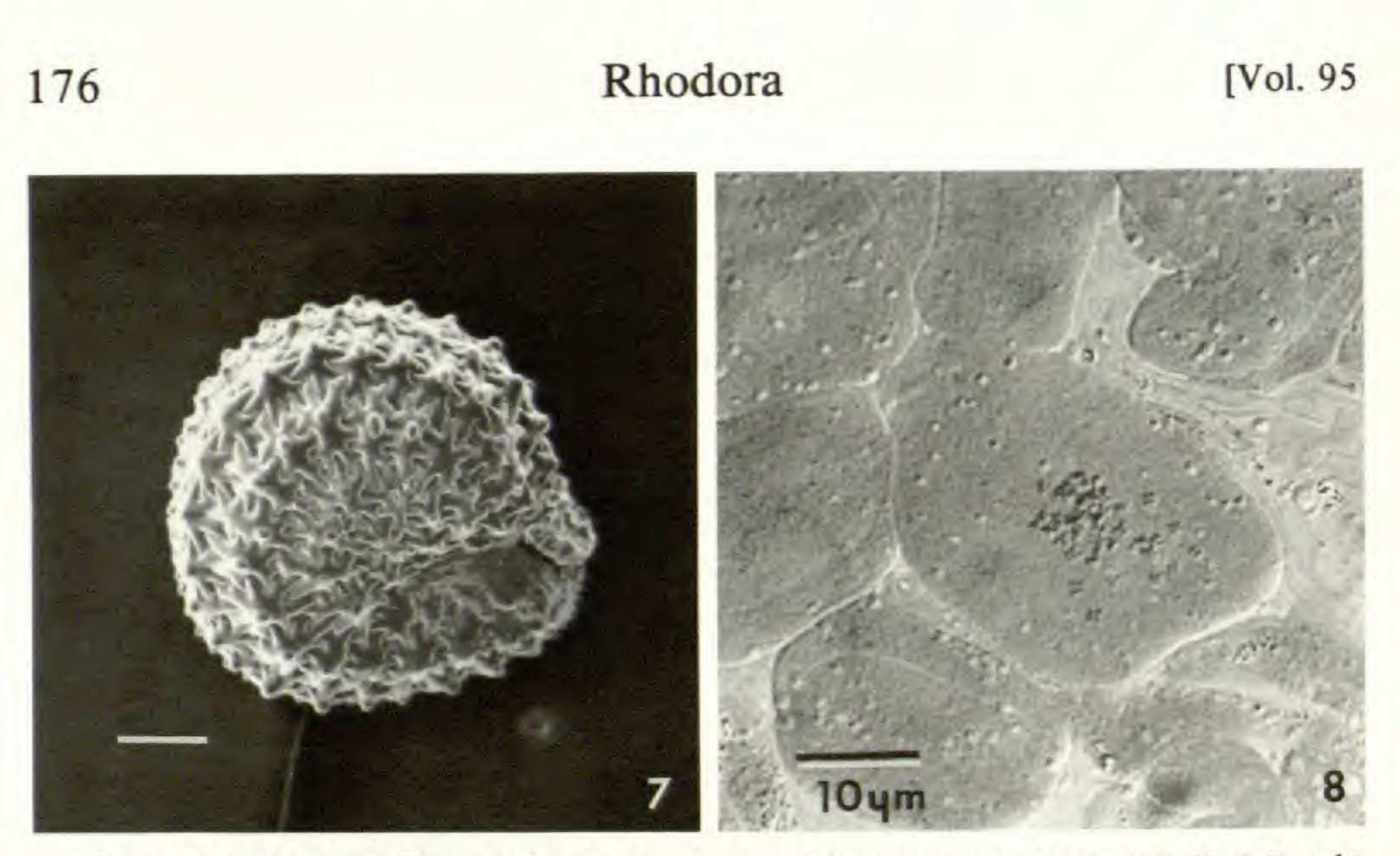


Figure 7. Stellate (S-undulate) pattern with definite tubercles, labelled P. oleracea.

Figure 8. Root-tip squash showing 2n = 36 in *P. oleracea*.

Texas. This plant is also P. retusa, but the point at which it was attached to this sheet is uncertain. Sheet 2 has several pieces of plants, including seeds, with Engelmann's handwriting: "From Texas seeds, cultivated St. Louis." Sheet 3 has one large top of a plant, with Engelmann's handwriting: "From Texas seeds, cultivated St. Louis." Seeds are present. Sheet 4 has one large top of a plant, with a label not written by Engelmann: "Texas seeds." Seeds are present. Sheet 5 has one large top of a plant, has an Englemann handwritten label: "From Texas seeds, cultivated." Originally the specimen was at Princeton University but was acquired by NY in 1945. There are no seeds on this specimen, which Legrand annotated as var. retusa in 1949. Sheet 6 is a mixed collection. At the top are two small, whole plants annotated by Legrand as P. lanceolata. Below are the tops of two plants of P. retusa, below which is Engelmann's handwritten label: "From Texas seeds, cultivated." There are two packets of seeds, one at the top and one at the bottom. Sheet 7 has the tops of several plants, has a personal label in Engelmann's handwriting: "From Lindheimer's Texas seeds, cultivated." Seeds are present. Sheets 1 and 7 are the most documentable specimens. Sheets 2 and 3

have no dates, although the date can be implied due to the sequence of numbers. Sheet 4 does not have an Engelmann personal label. Sheet 5 does not have any seeds. Sheet 6 is a mixed collection. Since Engelmann's work was in St. Louis, we designate

Table 2. A comparison of the number of specimens showing the overlap of secondary morphological characteristics used to separate *P. retusa* from *P. oler-acea*.

Specimens Labeled	Seed Size 0.9 mm or More	Seed Size Less Than 0.9 mm	Winged Sepals	Unwinged Sepals
P. retusa	83	38	103	18
P. oleracea	58	222	111	169

the first specimen, numbered 8871, as the lectotype: UNITED STATES, from Texas seeds, cultivated St. Louis, Aug 1849, *Engelmann s.n.*, мо!, isolectotypes: мо!, GH!, NY!.

Notwithstanding this lack of a holotype, this suite of six specimens (one had no seeds) had the same seed surface characteristics. From our group of 121 specimens labelled P. retusa, 59 specimens had the combined raised stellate and tuberculate condition. The others showed various combinations of transitional morphologies, ranging from raised stellate with no tubercles to tuberculate without the stellate pattern. As we examined over 1300 specimens labelled P. oleracea, we found 280 specimens with seed surfaces that approached the concept of P. retusa. We looked at all specimens with tuberculate or stellate surfaces in an attempt to correlate seed size larger than 0.9 mm, retuse leaf apex, winged (carinate) sepals around the capsule, obtuse vs. acute sepal tips and no. of stigmas/styles, other morphological features that have been used as secondary identifying characteristics in the various treatments cited above. In this broad-leaf group of species, there are many specimens that were well prepared during drying, with packets containing leaves and fruits. We were able to compare the characters enumerated above with the seed surface patterns. The retuse leaf apex is completely unreliable. To illustrate the lack of consistency in the other two characteristics, Table 2 shows the comparison of these features. Many of these 280 specimens were identified originally as either P. oleracea or P. retusa and later annotated the reverse. We could find no consistency in the shape of the sepal tips nor a definitive number of stigmas/ styles. Checking for stigmas/styles in dried portulacas is not very accurate however. Figures 4, 5, 6 and 7 illustrate some of the intermediate patterns of the seed surfaces, which bridge the gaps between Figures 1, 2 and 3 (Table 3). Figures 1 and 2 from the

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Table 3. Voucher data for representative specimens of Portulaca used for SEM of seed surfaces.

- Fig. 1. P. oleracea L. Louisiana: Rapides Parish, 19 Jul 1979, Pias 4345 (NLU).
- Fig. 2. P. oleracea L. Alabama: Mobile Co., 26 Aug 1965, Deramus D732 (ALU).
- Fig. 3. P. retusa Engelm. Texas: Williamson Co., 16 Aug 1961, Walker 73 (TEX).
- Fig. 4. P. retusa Engelm. Arizona: Apache Co., 2 Sep 1984, Mohlenbrock 2434 (ASU).
- Fig. 5. P. retusa L. Arizona: Navajo Co., 1897, Zuch s.n. (US).

- Fig. 6. P. retusa Engelm. Arizona: Pinal Co., 8 Sep 1929, Kearney 6002 (ARIZ).
- Fig. 7. P. oleracea L. Texas: Garza Co., 29 Jul 1967, Hutchins 1354 (SMU).

southeast show the granulate and obscurely stellate patterns respectively. Figure 3 is the typical "P. retusa" type. Figure 4 shows the beginning of the raised stellate pattern, with Figure 5 showing an increase in height. Figure 6 shows a tuberculate pattern emerging from a granulate surface, while Figure 7 shows the beginning of a tuberculate pattern from a completely stellate (no granules), which then merges into Figure 3. Other transitional surfaces can be found, but these serve to show the clinal variation.

Legrand (1962) specifically discussed the concept of P. retusa. He dismissed all of the morphological features (seed size, winged sepals and number of stamens) as being influenced by the environment and the season at the time of development. He also noted that there were transitional seed surface patterns between P. oleracea and P. retusa, saying that he had seen these same forms in plants from the provinces of Salta and Cordoba in Argentina. We observed on specimens he annotated early in his study that he considered P. retusa to be a variety of P. oleracea. A specimen from NY was annotated in 1949 as var. retusa, but by the time he published his monograph in 1962 he had lost confidence in the seed surface characteristic and failed to recognize P. retusa as a variety.

Since Engelmann originally cited the granitic region of west Texas as the type locality, we checked the 121 specimens with well defined stellate-tuberculate seed surfaces for habitat and geographic distribution. There were no habitat correlations, the plants being associated with alluvial soil, clay meadows, rocky slopes, granite, rhyolite, limestone, gypsum and dolomite. Geographi-

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cally the specimens were distributed from central TX up through the panhandle of TX into OK, southern KS and CO and westward into southern NM and AZ, with transitional forms into the Mojave Desert of CA.

Because of the lack of predictable and persistent morphological features, including seed surface, we conclude that P. retusa is a part of the polymorphic P. oleracea.

TOLOGY

Portulaca is characterized by a sequence of polyploids, particularly in the more geographically widespread species (Matthews et al., 1992a, 1992b). Portulaca oleracea shows this sequence also, from a base of X = 9. There are diploid races (2n = 18) in Africa (Hagerup, 1932), Central and North America (Danin et al., 1978); tetraploid races (2n = 36) in India (Khullar and Dutta, 1973), Central and North America (Danin et al., 1978) and hexaploid races (2n = 54) in India (Khullar and Dutta, 1973; Sanjappa, 1978), Africa (Hagerup, 1932; Bouharmont, 1965; Boquar, 1986; Nyananyo and Okoli, 1987), in Europe (Walters, 1964; Bouharmont, 1965) and in North America (Cooper, 1935; Steiner, 1944; Heiser and Whittaker, 1948; Mulligan, 1961; Danin et al., 1978) and Hawaii (Kim and Carr, 1990). In addition, Sharma and Bhattacharyya (1956) reported 2n = 45 from India and Sugiura (1936) reported 2n = 52 from Japan. The North American counts of 2n= 54 have been scattered geographically from Wisconsin (Cooper, 1935), Virginia (Steiner, 1944), California (Heiser and Whittaker, 1948; Danin et al., 1978), Ontario (Mulligan, 1961). In addition, Danin et al. (1978) reported 2n = 36 from California. Danin and Anderson (1986) reported in their study of the subspecies of P. oleracea in Florida the occurrence of 2n = 18, 36 and 54. No counts were made for this study but numbers were projected based on the previous report by Danin et al. (1978) correlated with the identification of the subspecies.

We wanted to determine the chromosome number from a variety of geographic areas to determine if a correlation existed between geography and cytology, when compared to the above data. We also wanted to publish a photograph of the chromosomes for a North American collection. Photographs of the chromosomes of P. oleracea are scarce in the literature. Some early reports were accompanied by camera lucida drawings (Cooper, 1935;

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Steiner, 1944). There is a photograph of a meiotic figure by Kim and Carr (1990) from Hawaii. Danin et al. (1978) provided the most comprehensive study of the North American distribution, but published no photographs to document the counts. We can understand the reason for this. After a survey of 20 plants from CA, NM, IL, NC and SC involving over 250 root tip preparations we have been unable to achieve a high quality figure for photography. Baquar (1986) stated, "The chromosomes in general are tiny, threadlike, forming clusters and are difficult to spread for

karyological studies." Our results are not different from these other investigators. Only two other papers have photographs of the chromosomes of *P. oleracea*; Khullar and Dutta (1973) from India and Nyananyo and Okoli (1987) from Africa. We were able to obtain 10 counts of 2n = 54 from IL. Ninety-one counts from CA, NM, NC and SC were 2n = 36. There appears to be a tendency for the hexaploid (2n = 54) to occur in the northern part of North America. However before any conclusions can be drawn, further counts from the United States and Canada would have to be made, and these should be compared to the counts from upper latitudes in Europe. Counts of 2n = 54 have been reported from Africa and India. The best figure we produced is shown in Figure 8, a 2n = 36 from SC. Voucher specimens are on file at UNCC.

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